

## CENTRE

Data have been collected, collated, and cleaned. As has become a 5-year ritual, results became available earlier this year from the census of the Barro Colorado Island (BCI) Forest Dynamics Plot. This marks the completion of the fourth census of the 50-ha plot on BCI, Panama.

This census revealed several surprises. Most striking to me is the continuing decline of the

have seen in the last census continue to reflect the impact of a strong drought in 1982-83, which resulted from an El Niño Southern Oscillation event. During first recensus interval, the drought led to the death of many adult trees. Increased treefalls created many new gaps, which provided the opportunity for elevated recruitment. Now, 10-13 years later, mortality in the large size classes has decreased

## DISCOVERING

LETTER FROM THE DIRECTOR

## LONG-TERM



*Elizabeth C. Losos, Director, Center for Tropical Forest Science*

## PATTERNS

recruitment rate, which has fallen by half over the course of our plot censuses (Figure 1). The plot now has fewer stems than ever — 230,000 compared to 244,000 in 1990. (We were so surprised that we reconfirmed this result by rechecking recruits over a large portion of the quadrats.) And, for the first time since the establishment of the plot, the mortality rate for all stems  $\geq 1$  cm is greater than the recruitment rate. Interestingly, when examining mortality by size classes, we see that its increase is due to the high level of mortality within the smallest size class (Figure 2). Thus, the BCI forests could be characterized, at least within the time scope of our study, as in a state of disequilibrium.

Why such dramatic changes in mortality and recruitment? I suspect that the changes that we

while it has increased in the small size classes, perhaps due to the strong competition among small trees that are fighting for a place in the canopy.

While further testing and analyses need to be done to better understand the results from the fourth BCI census, there are several basic lessons to be learned from our experience thus far. First, long-term studies are critical to understanding tropical

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FEATURE



# SPATIAL PATTERNS OF HURRICANE DISTURBANCE IN A 16-HECTARE PLOT IN THE LUQUILLO EXPERIMENTAL FOREST, PUERTO RICO

Edwin M. Everham III, Radford University

On September 19, 1989, Hurricane Hugo passed over the eastern end of Puerto Rico (Figure 1), unleashing a category-4 hurricane with maximum winds reaching up to 166 km/hr. Nine months after Hurricane Hugo, a 16-ha Hurricane Recovery Plot (HRP) was established in Luquillo through collaboration of Radford University, Manomet Observatory for Conservation Sciences, and the University of Puerto Rico to assess hurricane damage and monitor recovery dynamics.

The Hurricane Recovery Plot at Luquillo is 320 m x 500 m and cuts across two watersheds. In 1990, each tree  $\geq 10$  cm dbh within the plot was identified, tagged, measured, mapped, and assessed for hurricane damage. In 1993, we completed a second survey of stems down to 1 cm dbh. In 1995, we initiated a recensur of the entire plot, which is due to be completed in August 1996.

Due to prior human disturbance, none of the plot can be considered to contain primary forest. The southern portion of the plot was subject to stand improvement cutting in 1937 and 1946. Additionally, timber harvests from between 1944 and 1953 removed approximately one-half the volume of *Dacryodes excelsa* (Burseraceae), commonly known as tabonuco. Having been left undisturbed since this time, the southern portion of the plot now resembles virgin stands of tabonuco. By contrast, the northern portion of the plot was subject to more extensive human disturbance. An aerial photograph from 1936

1. Stems snapped off above ground.
2. Stems uprooted.
3. Stems broken at the ground but not uprooted.
4. Stems bent by the wind or other treefalls.
5. Stems that did not receive any of the previous four types of damage, but did have visible damage to branches  $\geq 10$  cm dbh.

reveals that the northern portion of the plot was once subject to clear-cutting for agriculture, resulting in 20 - 80% loss of forest cover. This area of the plot currently supports secondary forest dominated by *Casearia arborea* (Flacourtiaceae) (Figure 2).

The initial survey of stems  $\geq 10$  cm was carried out quickly in order to be able to assess the damage caused by the hurricane. Hurricane damage was quantified in four categories. First, we measured damage as counts of stem mortality. Second, we recorded

stem damage by assigning each tree to one of five mutually exclusive stem damage categories (see box). Third, we assessed basal area loss per quadrat and subquadrat, which was calculated by combining data from categories one and two — all stems either damaged or killed. Finally, we measured damage to the post-hurricane canopy by assessing the

height of the canopy at each 5-m subquadrat grid points between April to July of 1992.

Since data were collected over a gridded plot, both quadrat variance models (using quadrat or subquadrat data) and distance models (using x, y coordinates) are applicable for examining spatial patterns of hurricane damage. Using the maps generated from different categories of hurricane damage, we determined patch size frequency distributions of damaged areas and converted these distributions to proportion of total area

HURRICANE  
DAMAGE  
RESULTS IN  
UNIQUE  
RECOVERY  
DYNAMICS

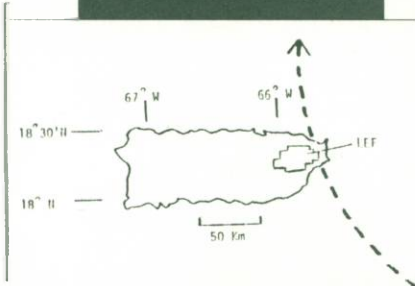


Fig. 1. Map of Puerto Rico and the location of Luquillo Experimental Forest. Arrow denotes hurricane path.

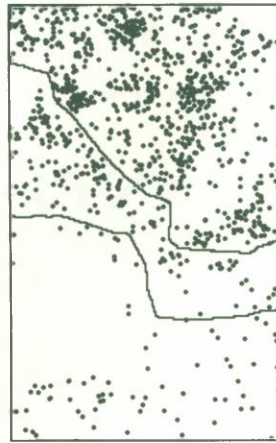


Fig. 2. Distribution of *Dacryodes excelsa* (right) and *Casearia arborea* (left) in the plot. All stems  $\geq 10$  cm dbh, alive before Hurricane Hugo, are mapped.

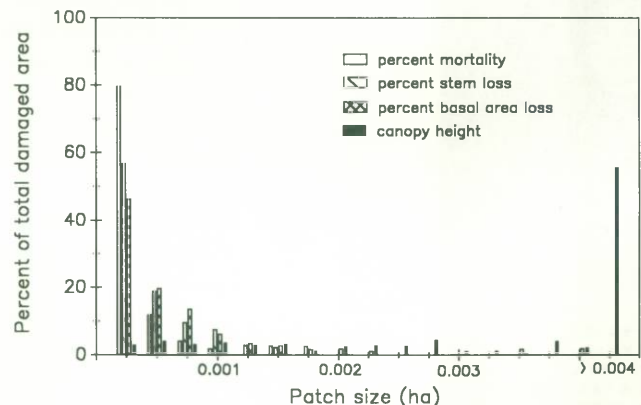


Fig. 3. Patch size and frequency distribution. Proportion of the total area of damage in each patch size.



damaged (Figure 3).

A total of 13,078 live stems  $\geq 10$  cm dbh of 88 tree species were assessed for damage during the first census. Since the HRP was established nine months after Hurricane Hugo, we assumed that all recent damage and mortality were caused by the hurricane. Of the assessed stems, 16.7% had stem damage. Of the remaining 83.3% that did not receive stem damage, 15.4% received major branch damage. Mortality apparently caused by the hurricane was 9.0%, 30 months after the passage of Hugo. Overall, 18.6% of the basal area was damaged to some degree.

The patterns of hurricane damage differed between the northern and southern ends of the plot, with stem damage concentrated in the north and branch damage concentrated in the south. The southern end of the plot received a higher degree of branch damage possibly because it is composed mainly of primary forest whose species appear to be more resistant to stem damage and mortality, though they tend to shed branches in a hurricane.

The distribution of damage, as measured by all four categories, is significantly clumped and the patch sizes are concentrated in the smallest size measured (0.0025 ha). The spatial pattern of hurricane damage suggests that catastrophic wind disturbance is similar to treefall gap formation, since patches of damage are concentrated in the smallest sizes. However, there are several distinctive characteristics of hurricane disturbances. For example, loss of branches disrupts the canopy and may create gaps, without corresponding damage to stems. Additionally, though not captured in any measures examined in this paper, hurricane damage also results in extensive defoliation. This defoliation has several corresponding effects: 1) greater shifts in abiotic gradients, such as light, than would be associated with a treefall gap; 2) system-wide pulses of litter and woody debris which could influence the nutrient availability and germination and seedling survival during recovery; and 3) shortages of seeds and seed dispersers over large regions. These effects, together with the occasional larger patches of damage created by hurricanes, result in unique recovery dynamics.

The results of this study indicate the importance of tree community data, previous disturbance history, and the influence of disturbance on tree communities. The spatially explicit grid structure allowed us to illuminate the fine-scale patch structure and heterogeneity of hurricane disturbance. The ability to predict patterns of severity of hurricane damage on large scale communities is dependent on detailed distribution data of the species and their susceptibilities to wind disturbance. These predictions are critical in understanding the long-term stand-level dynamics in hurricane prone areas. ■

## WAORANI HUNTING AND HARVESTING PRACTICES IN ECUADOR

Fabian Rodriguez, CTFS/STRI

One of the objectives of the Center for Tropical Forest Science (CTFS) and its partners is to gain an indepth understanding of highly diverse forests, such as those in the Amazon. A fundamental component is a strong knowledge of forest community and structure. This led to the establishment of a network of Forest Dynamics Plots, such as the 50-ha plot in Yasuní National Park, Ecuador. In collaboration with the Catholic University of Ecuador and the University of Aarhus, Denmark, enumeration of the plot has been carried out since January 1995. A second objective is to better understand the interactions between humans and forest. In this article, I will discuss a socio-economic study in which I investigated the local uses and level of consumption of non-timber forest products that are found in the buffer zone of Yasuní National Park. The results of this study will later be compared and incorporated with data from the 50-ha Forest Dynamics Plot. This study was carried out under the guidance of CTFS and with technical assistance from EcoCiencia, an Ecuadorian non-governmental organization.

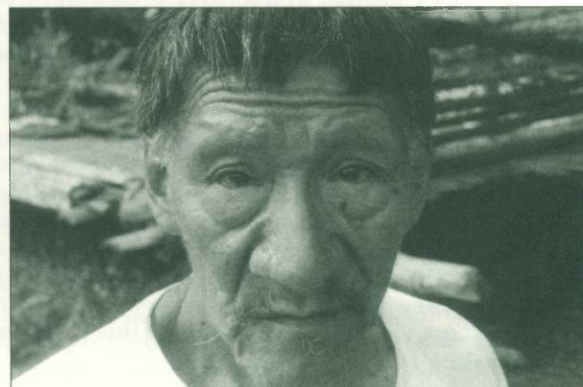
One of the largest local indigenous groups living within and around Yasuní National Park are known as Waoranis. This socioeconomic study focused on the degree to which access to economic markets affects the local Waorani's use of tropical forest products. We carried out research within three Waorani communities: Cacataro, Tiguino, and Quehueiri-ono, all located in the buffer zone of Yasuní National Park between the Shiripuno and Tiguino rivers. Using household surveys, we documented Waorani preferences in hunting and harvesting practices. In comparison to previous ethnobotany and ethno-zoology studies that have aimed to construct exhaustive lists of forest products used by Waorani communities, the present research focused more on the relative consumption of forest products.

Though Waoranis are historically hunters and gatherers, this lifestyle has become increasingly vulnerable. Their customs and traditions are rapidly changing due to the influence of outside cultures. Clear evidence of the impact of outside influence includes: 1) their change to a sedentary lifestyle; 2) their change to a political system with

community leaders; 3) and their adoption of outside and more efficient technologies for harvesting and hunting. Despite these radical changes, many Waoranis still maintain an intimate knowledge of forest ecology, including an understanding of the interdependence of animal and plant cycles. This complex understanding has come to the attention of many anthropologists, botanists, and social scientists who are interested in the wealth of unwritten knowledge the Waoranis possess.

Our study determined that the three studied Waorani communities consume, on a monthly basis, a wide array of plant species consisting of 31 families and 76 plant species. The most frequently used family was the palm family (Arecaceae), with a total of 11 species utilized. For example, the leaf fibers of *Astrocaryum chambira* is used by indigenous people to make hammocks and handbags (shigra), which are traded in the cities of Francisco de Orellana (Coca) or Misahualli. Waoranis use another palm, *Iriartea deltoidea*, to make blowpipes, which were once an important hunting tool though now they are primarily sold as crafts. Other important families were Cecropiaceae, Rubiaceae, and Sterculiaceae, each consisting of three species. Waoranis use forest plant products mainly for food sources, accounting for 60.1% of all species recorded. The second most important use was "craft and tool" category, which included natural fibers and tints, crafts, poisons such as barbasco (*Lonchocarpus nicou*) to catch fishes and curare (*Curarea tecunarium*) for hunting. Crafts and tools accounted for 17.5% of all species recorded. Construction materials comprised 13.1%, which includes the annual renovation of houses due to termite damage. Fuelwood accounted

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Yewa, the oldest member of the Waorani community.



## WAORANI USE OF FOREST...

Continued from page 2

for only 4.8% of all species, but this does not take into account that Waorani people often re-use the wood from former houses as fuelwood. Finally, medicinal plants represent only 2.9% of all species harvested.

Though Waoranis use forest products extensively, the majority of their food comes from agricultural crops. Waorani communities raise crop products such as manioc (yucca), bananas, hard corn, peanuts, and some fruits like papaya and pineapple.



Waorani family in front of traditional style house.

Manioc and bananas comprise a high proportion of their diets. They use an average of 15.6 kg/week of manioc to prepare "chicha," an alcoholic beverage, and an average of 21.5 kg/week of platano, the local name for bananas. Within the three surveyed communities, the harvest is mainly carried out by women (59.4%), although men also participate in this activity (40.6%).

Waoranis are also active hunters, especially of mammals. Among them, the common woolly monkey (*Lagothrix lagotrichia*) was the most important prey hunted in all three communities. The collared peccary (*Tayassu pecari*), the Amazon red brocket deer (*Mazama americana*), and the agouti (*Agouti paca*) were also often hunted by these communities. The most valuable prey among birds were the Spix's guan (*Penelope jacquaca*), Salvin's curossaw (*Crax salvini*), and the Cuvier's toucan (*Ramphastus cuvieri*). The

black caiman (*Caiman crocodilus*) was the most hunted prey among reptiles. Also, due to their recent migration closer to riparian environments, fishing has recently become popular within Waorani communities. Some members of Quehueiriono community have specialized in this activity because fish are relatively easy and less time-consuming to catch. Additionally, any member of the community can participate in this activity.

The influence of market on Waorani communities is evident in the amount of products extracted per community. Statistical analysis of timber extraction, hunting, and harvesting activities within the three Waorani communities reveals that communities that are closest to the

markets harvest and extract larger amounts of forest products. As the market pressure increases, it also increases the demand for forest products. Hence, communities in close proximity to markets will extract and harvest more forest products, especially timber. For example, Cacataro and Tiguino, which are close to active markets, harvest more forest products than Quehueiriono, which is located the farthest from active markets. This does not necessarily mean that Quehueiriono does not extract timber products. Although Quehueiriono is the farthest from a market, it is located on the Shiripuno River, facilitating access to markets. Therefore, we conclude there is an inverse relationship between distance to market and extraction and harvesting of forest products, but access to market, such as roads and rivers, confounds this relationship.

## DISCOVERING PATTERNS...

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forest dynamics. Even 13 years is not long enough to unravel many of the complex processes operating in the BCI forest. Second, the inclusion of small size classes has equipped us with a sensitive tool for detecting changes in demography. Had we limited our study to larger trees, such changes may not have been discovered for decades, if ever. Third, our large sample size — close to 250,000 individuals of over 300 species — has provided us with a high level of statistical confidence in our results. For example, we have been able to run population-level analyses for almost 150 species, each species represented by more than 100 individuals.

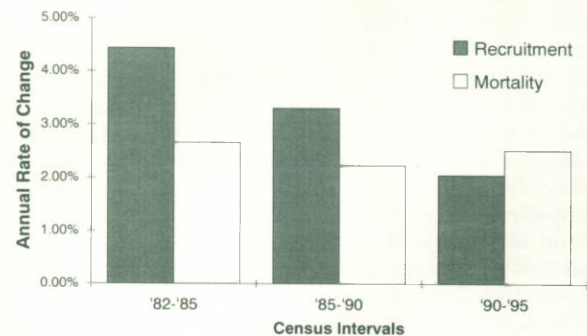


Fig. 1. Recruitment and mortality in BCI Forest Dynamics Plot.

Finally, additional long-term samples from the same region — presumably in areas that experience similar climatic events such as the drought of 1982-83 — would be useful for comparative studies. Alas, BCI houses the only large Forest Dynamics Plot in Panama. However, over the last few years, the Center for Tropical Forest Science has begun to establish a series of smaller plots within the Panama Canal area, following the same methodology used for the large Forest Dynamics Plots. Additionally, a growing number of large Forest Dynamics Plots throughout the tropics allows comparisons across biogeographical regions.

BCI plot census results have provided invaluable biological data that have directly fueled a large body of analyses and hypothesis testing. The plot has also been used, however, for much broader scientific purposes. Over the years, the community and species-specific demographic information have catalyzed a wide variety of complementary basic and applied research. In this issue of *Inside CTFS*, we feature a sample of some of the recent research that has been carried out

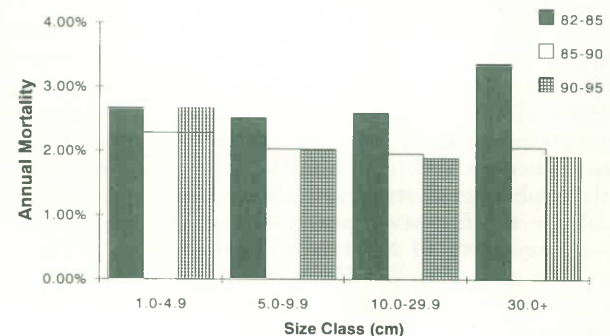


Fig. 2. Tree mortality in BCI Forest Dynamics Plot.

directly or indirectly using data generated from the plot. Patterns are becoming clearer with the completion of each new census and each complementary project — not only from BCI, but from the CTFS sites around the globe.



# THE FIRST FOREST DYNAMICS PLOT

Traditionally, long-term monitoring plots in the tropics have focused primarily on large stems, often in relatively small tracts. While such plots produce critical data to address some ecological issues, they are insufficient for others. Dr. Stephen Hubbell (Princeton University) and Dr. Robin Foster (STRI and The Field Museum) realized that, to address many questions related to forest dynamics and regeneration in diverse tropical forests, bigger plots would be needed that included trees of smaller size classes. Thus in 1980, with support from the US National Science Foundation, Drs. Hubbell and Foster lead a team of researchers in the establishment of the first 50-ha Forest Dynamics Plot, which included all free-standing woody vegetation with stems 1 cm dbh. They selected a site on the central plateau of Barro Colorado Island (BCI), Panama, at 150 m above sea level (Figure 1). The plot is situated on relatively level terrain, though it contains 3-10% grades on the eastern and southern margins and a small seasonal swamp in the middle.

The first census was completed in 1982. All stems were tagged, identified to species, measured for diameter, and mapped, totaling 235,349 individuals of 304 species. Second, third, and fourth complete censuses of the plot were carried out in 1985, 1990, 1995, at which time growth, mortality, and new sapling recruitment were recorded. In addition to tree demography, data have been collected annually since 1983 on the dynamics of canopy height on a 5-m grid over the entire plot.

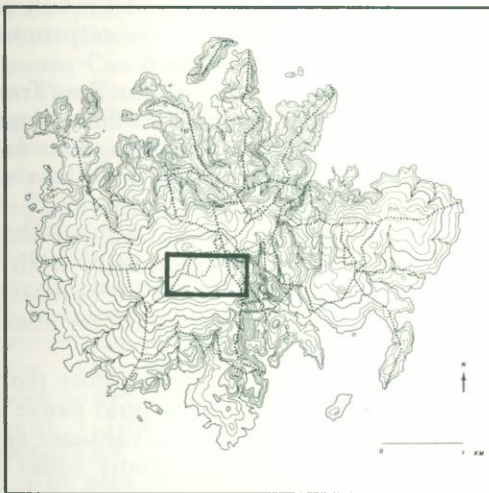


Fig. 1. Barro Colorado Island and location of 50-ha Forest Dynamics Plot.

The canopy height has enabled the measurement of demographic variation for each species under gap and shaded conditions. Beginning in 1994, a seedling and small sapling census (all woody plants between 20 cm height and 1 cm dbh) has been initiated, with the

goal of a 4% stratified sample of 1 m<sup>2</sup> in every 5 m x 5 m quadrat.

Dr. Richard Condit, CTFS Latin American Coordinator since 1992, has played a critical role overseeing the BCI Forest Dynamics Project and leading the data analyses for the plot. Drs. Condit, Hubbell, and Foster continue to participate in the censuses and research within the BCI Forest Dynamics Plot. They are supported by an increasingly skilled team of botanists, mappers, data-entry staff, and technicians, headed by field leaders Rolando Perez, Andres Hernandez, Salomon Aguilar, Milagro Ruiz, and data-manager Suzanne Loo de Lao. The experience and

expertise of the field staff has led to great efficiency and accuracy improvements since the first census: In the most recent recensus, a final database was finished just 14 months after the field work began.

Results from the initial census and three recensuses of the Forest Dynamics Plot on BCI have already made an impact on our understanding of tropical forest dynamics and the maintenance of species diversity. Data from that plot suggest that the species assemblage in the BCI forest is not in equilibrium but rather in constant flux, and that many species are generalists rather

## At a glance: Barro Colorado Island, Panama

Barro Colorado Island (BCI) is unique. Once a hilltop, the island was created by damming the Chagres River in the early 1900's to build the Panama Canal. During canal construction, a number of scientists were dispatched to Panama to study insect-vectors of tropical diseases. Realizing the value of studying tropical plants and animals under natural conditions, several scientists petitioned the Governor of the Canal Zone to designate BCI a protected area. In 1923, the island became one of the first biological reserves in the New World. After the second world war, the Smithsonian Institution was given the overall responsibility of managing BCI as "the Canal Zone Biological Area," which evolved and expanded to become the Smithsonian Tropical Research Institute (STRI) in the mid-1960s. Today STRI also has custodianship of the five adjacent mainland peninsulas which together with the island make up the 5400 hectare Barro Colorado Nature Monument (BCNM).

Over the past three-quarters of a century, BCI has become one of the most intensively studied forests in the tropics. This 15 km<sup>2</sup> island is completely forested, half with "old growth" forest that has not been cleared for agriculture in recent history. Classified as tropical moist forest, BCI receives about 2600 mm of precipitation annually, distributed mainly between May and December. BCI contains a network of 59 km of marked and protected trails and is home to a recorded 1316 plant species, 381 bird species, and 102 mammal species.

than niche specialists. On BCI, the level of species diversity and composition of that forest appears to result from chance and historical factors more than from unique attributes of individual species. Results from the BCI plot have also made important applied contributions to restoration ecology and local forestry in Panama. For example, fast-growing species for reforestation have been selected using growth data from the plot, and community-based trials for native species reforestation of degraded pastures are currently being implemented. A bibliography of publications from the Forest Dynamics Plot on BCI and at other sites can be found on the CTFS World Wide Web homepage (<http://www.si.edu/organiza/centers/stri/forest/ctfs.htm>) or can be obtained by writing the CTFS office in Washington, DC (see page 16 for address).

Since the establishment of the plot on BCI, forest dynamics research has developed a global dimension through the formation of partnerships with other long-term, forest-research enterprises worldwide. The CTFS now links 13 such compatible programs. The strength of the plot research on BCI is reinforced by equally rigorous, comparable studies conducted in other branches of the CTFS network and, together with them, is developing the power to understand how forests are changing and how forests can be conserved and better managed worldwide.

# MANAGEMENT OF A LARGE DATABASE DURING A RECENSUS

*Suzanne Loo de Lao, CTFS/STRI*

The fourth census of the 50-hectare Forest Dynamics Plot at Barro Colorado Island, Panama, was completed last year. The field work started in January 1995 with 12 workers and 4 supervisors, and ended approximately 10 months later. Diameter measurements of the larger buttressed trees took one more month with a reduced work force. A total of over 260,000 plants were censused.

The data sheets and maps used in the census were printed out and ready before the census started. Data entry began in May, once mappers had recensused a substantial number of columns within the plot and one of the supervisors had reviewed the corresponding data sheets. The FoxPro data-entry program was designed to display as many records as possible on the screen, instead of only one record at a time. This allowed the people entering the data to know exactly where they were on the data sheet and permitted easy data verification. Also, macros were used to save keystrokes for repetitive fields.

Some screening and validation were designed into the data-entry program. For example, dbh measurements had to be within a certain range, species codes had to match with a list of existing codes, dates had to be within the census period, and quadrat numbers and codes had to be valid numbers and codes. Besides catching data-entry errors, this screening helped find errors made in the field which the supervisor had not detected. Data-entry was initiated while field work was still underway, so that any necessary checking could be done in the field. A list of these errors was sent back to the field once a month for the supervisors to correct. Double data-entry was performed to detect and correct typing errors.

To assess and reduce the level of measurement errors made by field workers, thirty-three 20 m x 20 m quadrats were chosen at random and remeasured by a different worker. Field workers were not notified that their work would be checked so as not to bias them to be more careful when they were working in those quadrats. All plants  $\geq 10$  cm dbh were remeasured in these 20 m x 20 m quadrats. Within two 5 m x 5 m subquadrats of each 20 m x 20 m quadrat, all plants  $\geq 1$  cm dbh were remeasured. Remeasurements were taken within three weeks of the first measurement, because some plants grow rapidly.

We also checked dbh measurements against data collected in 1990. Extreme growth rates were rechecked. This was done separately for each half of the plot to avoid waiting until the end of the census. Taking an equal number of stems from each doubling size class, over 1100 dbh measurements (0.5% of all plants) were rechecked, accounting for the most extreme negative and positive growth rates. We found that 29% of these measurements had been incorrectly measured in the census, 24% were resprouts which had not been coded as resprouts, 23% were apparently due to measurement errors in the previous census, and 21% were correctly measured.

Data-entry took 7.5 months, about 2600 person-hours, to complete using two 286 IBM-compatible computers. All the data sheets were entered and the maps digitized by December 1995. Data entry itself does not require powerful machines, but faster machines are recommended for error checking, calculations, and data analyses after all the data have been entered and merged into one large database.

Once data-entry was finished, the database was "cleaned up." Every plant record was checked to make sure it had a location, species code, date of measurement, tag number, dbh measurements for every multiple stem, and point of measure (POM) if not at 1.3 m (the standard height at which dbh is measured). Corrections were made to misidentified species; tags were eliminated from previous censuses if duplicate tags were found; location changes were made to those plants which had been incorrectly mapped previously; and plants presumed dead previously but now alive had their "dead" code removed.

As part of the clean-up process, we determined for each plant whether the POM changed. This is very important for comparing dbh measurements to previous censuses. We can calculate growth rates only for those trees whose POM is the same in the two censuses. Examples of POM changes occur when big-buttressed trees were measured at a different height from the previous census, when the main stem had broken off or died, and when a tree resprouted after the main stem died.

The updated BCI database including the data from the fourth census is now ready. During the final stages of the cleaning process, errors kept appearing that had to be corrected. We cleaned the database as best we could, then stopped entering any more changes and presented this database for analyses. We will always find errors if we look hard enough, especially with a database this large. The database will be regularly updated, once a year or once every two years for example, with all errors accumulated until then.

During the first two censuses at BCI, many more codes were used to explain the condition (and cause of the condition) of the plants. There are advantages and disadvantages to this. When there are many codes to learn, field workers are more prone to make mistakes. It is better to have as few codes as possible and make them as simple as necessary for the field work. However, more codes do help explain some discrepancies found at a later stage, such as why some dbh measurements decreased from one census to another or whether the POM changed. Codes also provide opportunities for additional types of analyses and studies.

Database management is a tedious, almost full-time job during a census or recensuse. However, once the database is complete and ready, and the requests for data and analyses start pouring in, it is exciting to study how the forest has changed in the last five years compared to the previous years, to verify the current theories, and to watch the unfolding of yet another chapter in the mysteries of tropical forest dynamics. ■

**DATA-ENTRY WAS INITIATED WHILE FIELD WORK WAS STILL UNDERWAY, SO THAT ANY NECESSARY CHECKING COULD BE DONE IN THE FIELD.**



# STRUCTURE AND COMPOSITION OF A SEMI-DECIDUOUS FOREST IN PANAMA

Andres de J. Hernandez, CTFS/STRI  
(Translated by Nadilia Gomez)

The 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI) has provided a wealth of information concerning the community dynamics and species demography of this particular forest. To expand this understanding, we would like to conduct studies that encompass a wider range of forest types under different climatic and edaphic conditions. Areas in close proximity to BCI offer an opportunity for such comparative studies. Within a short distance from BCI, there is marked variation in rainfall, soil type, and elevation. For this reason, the Center for Tropical Forest Science (CTFS) has begun establishing a series of smaller plots across distinct environmental gradients within the Panama Canal area to complement the 50-ha plot on BCI. In this article, I will discuss a small-plot established in a semi-deciduous forest, one of the first of a series of plots.

Between August and December of 1994, CTFS installed a 4-ha forest plot near the Cocoli River in the Panama Canal area on the Pacific coast of Panama. This area is within the belt of secondary forest flanking the Panama Canal. Its woodland, estimated to be 60-90 years old, contains many deciduous species and has a average canopy height 30 m. The climate at Cocoli is dry, receiving about 1,700 mm of rainfall each year.

The plot enumeration followed the same methodology of other large-scale Forest Dynamics Plots. In the initial stages, the 4-ha plot was divided into 20 m x 20 m quadrats, each of which was further divided into 5 m x 5 m sub-plots. All trees and shrubs with dbh  $\geq$  1 cm were marked, measured, and identified to species.

The results of this initial investigation

reveal a total of 8186 individuals from 174 species, 125 genera, and 47 families. It is interesting to compare these figures to forests which have a wetter, more humid climate, such as BCI. For example, an average of 4581 stems representing 168 species are found per hectare at BCI versus 2047 stems and 116 species per hectare at Cocoli. These results lend some support to the hypothesis which suggests that soil type and humidity are decisive factors in the evolution of ecosystems and their floral composition.

Regarding stem abundance at Cocoli, we find that three species — *Calyptrotrichia* sp. (Myrtaceae) with 651 individuals, *Coussarea curvigemma* (Rubiaceae) with 608 individuals, and *Protium tenuifolium* (Burseraceae) with 592 individuals —

constitute 23% of all stems recorded. By comparison, there were 85 species represented by less than 15 stems and 31 species represented by only one stem. In total, 67% of all species present are rare, that is, having 15 individuals within the plot.

Analyzing the large-sized trees, we find that *Anacardium excelsum* (Anacardiaceae) dominates the canopy at Cocoli. This species is characteristic of late successional dry forests. Another large, late-successional tree, *Canavillea platanifolia* (Bombacaceae), has stems of the largest diameter, reaching almost 1.5 m dbh. It is important to note that these two species are represented by very few individuals of small diameter and, as seen in Table 1, the relative density of these two species is low though their basal area is high. On

the other hand, *Brosimum alicastrum* (Moraceae), which is common in primary forests, has a high density, but low basal area at Cocoli. As the Cocoli forest matures further, *B. alicastrum* and many other mature forest species will likely take over the canopy.

*Faramea occidentalis* (Rubiaceae) which dominates among small-sized trees at Cocoli is also very abundant on BCI. This suggests that its density is not influenced by the age of the forest. By comparison, *C. curvigemma*, the second most abundant species at Cocoli, is commonly found within young forests and is scarce on BCI.

In the future, we hope to enlarge this study to include more plots in varying conditions. We also plan to encompass a wider array of geologic formations, soil types, and humidity zones. This will help expand our knowledge of the floristic composition and structure of tropical forests.

Table 1. Ecological Importance of the Species in Cocoli

	Number of Individuals	Relative Density *	Basal Area (m <sup>2</sup> )	Relative Dominance**
<b>Shrubs</b>				
<i>Calyptrotrichia</i> sp. (Myrtaceae)	651	38.45	0.38	5.18
<i>Sorocea affinis</i> (Moraceae)	463	27.34	0.24	4.15
<i>Clavija mezii</i> (Theophrastaceae)	172	10.16	0.07	1.26
<i>Hirtella racemosa</i> (Chrysobalanaceae)	113	6.67	0.05	0.86
<i>Rinorea lindeniana</i> (Violaceae)	77	4.54	0.02	0.50
<b>Small-sized Trees</b>				
<i>Coussarea curvigemma</i> (Rubiaceae)	608	18.81	0.84	13.94
<i>Faramea occidentalis</i> (Rubiaceae)	580	17.94	0.79	13.11
<i>Swartzia simplex</i> (Leguminosae)	190	5.84	1.38	22.90
<i>Alibertia edulis</i> (Rubiaceae)	254	7.85	0.34	5.64
<b>Medium-sized Trees</b>				
<i>Calycophyllum candidissimum</i> (Rubiaceae)	161	8.18	6.69	27.83
<i>Trichilia pleeana</i> (Meliaceae)	322	10.36	5.21	21.67
<i>Scheelea zonensis</i> (Palmae)	35	1.12	3.44	14.31
<i>Guarea glabra</i> (Meliaceae)	190	6.15	1.90	7.90
<b>Large-sized Trees</b>				
<i>Anacardium excelsum</i> (Anacardiaceae)	128	6.25	42.00	40.99
<i>Canavillea platanifolia</i> (Bombacaceae)	59	2.88	28.90	28.21
<i>Protium tenuifolium</i> (Burseraceae)	592	28.94	1.07	1.04
<i>Brosimum alicastrum</i> (Moraceae)	503	25.59	1.08	1.05
<i>Astronium graveolens</i> (Anacardiaceae)	272	13.30	2.01	1.96

\* Relative density was calculated as the number of individuals of a species as a proportion of all individuals of that life form.

\*\* Relative dominance was calculated as the total basal area of a species as a proportion of the total basal area of all individuals of that life form.

## ALLOMETRY OF 50 TREE AND SHRUB SPECIES ON BCI

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The relative size and shape, that is, allometry, of the trees and shrubs in a forest may be important in determining the outcome of competition and in determining forest structure and dynamics. Although the size and form of individual plants is strongly influenced by the environment, studies of tree growth and allometry also have demonstrated strong correlations — both within species and in groups of species — between bole diameter, plant height, crown size, tree age, biomass, and leaf area index.

The relationships between trunk diameter, height, and crown size were studied for 50 species of trees and shrubs in the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama. These 50 species comprise 78% of all stems within the plot and thus play a large role in the structure of the tree community. Five to eight individuals of each species were measured across a full range of size classes. An attempt was made to measure at least one individual of each species in each of the doubling diameter at breast height (dbh) classes, 1.0 to 1.9, 2.0 to 3.9, 4.0 to 7.9, ..., and  $\geq 32$  cm dbh. Individuals of each species were selected at random. Before measurement, every tree was carefully inspected and those that had died or had obvious physical damage to their height or crown were not included in this study. Within each species, linear regressions of  $\log_{10}$  transformed data were calculated for bole diameter on tree height, height to crown base, and crown area. For the 50 species measured (total  $n=311$ ), dbh was strongly correlated with height, crown area, and crown base ( $r^2=0.92$ ,  $p < 0.0001$ ;  $r^2=0.88$ ,  $p < 0.0001$ ;  $r^2=0.74$ ,  $p < 0.0001$ , respectively).

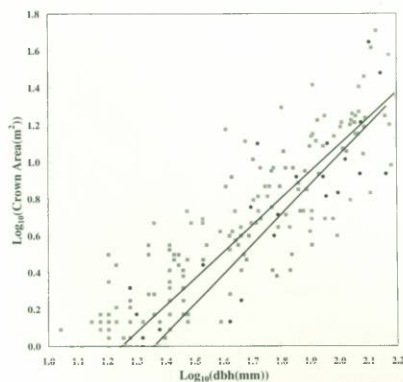


Fig. 1. Relationship between crown area and dbh for gap and non-gap species ( $1 \text{ cm} \leq \text{stems} < 16 \text{ cm dbh}$ ).

The data for plants  $\geq 1 \text{ cm}$  and  $< 16 \text{ cm dbh}$  were further divided into two sets of categories: 1) growth form (understory and overstory), based on maximum tree size and 2) regeneration requirements (gap dependent and non-gap dependent). The size range of  $1\text{--}16 \text{ cm dbh}$  ( $n=219$ ) was chosen to capture the change in allometry in trees before reaching the canopy. In this article, I discuss the results from one of these analyses, gap dependent versus non-gap dependent species.

No difference in crown area as a function of dbh was observed between gap and non-gap species as measured by regression analysis (Figure 1). In terms of the relationship between tree height and dbh, regression analysis detected no significant differences in slopes between gap and non-gap species, though the intercept of the gap species was sig-

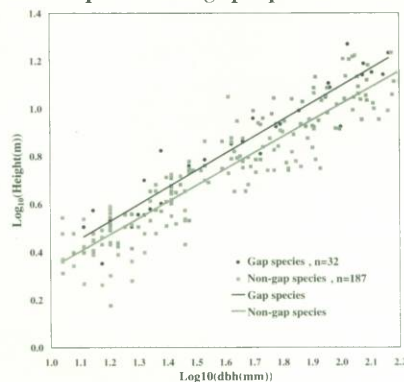


Fig. 2. Relationship between tree height and dbh for gap and non-gap species ( $1 \text{ cm} \leq \text{stems} < 16 \text{ cm dbh}$ ).

nificantly greater ( $p < 0.0001$ ) than that of the non-gap species (Figure 2). A similar analysis showed that the slope of gap and non-gap species did not significantly differ for the relationship between dbh and crown base, though the intercept of gap species was significantly higher ( $p < 0.001$ ) than that of non-gap species (Figure 3). These results suggest that species that require gaps for sapling growth and survival have an early height advantage (about  $1 \text{ cm dbh}$ ) over species that can grow and survive better in the shade. This height advantage is maintained for trees to at least  $15.9 \text{ cm dbh}$ .

Furthermore, gap dependent species  $\leq 16 \text{ cm dbh}$  had shallower crowns than the species that do not require gaps. Crown depth is calculated by subtracting the height of the crown base from the tree height. This finding may contradict one of

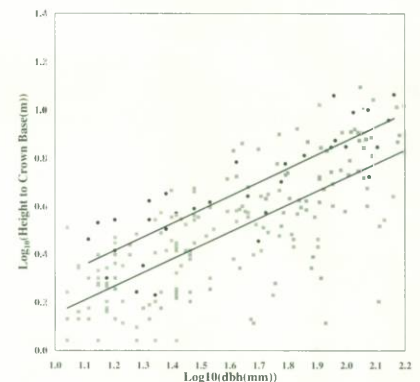


Fig. 3. Relationship between crown base and dbh for gap and non-gap species ( $1 \text{ cm} \leq \text{stems} < 16 \text{ cm dbh}$ ).

the predictions of Henry Horn's theory on secondary succession, which states that pioneer species should have multilayer canopies to capture as much light as possible, and shade tolerant species should have monolayered crowns to minimize self-shading in the light-deprived understory of the forest. However, gap dynamics in a mature closed canopy forest with advance regeneration is very different from secondary succession. In treefall gaps of closed canopy forests, light-demanding species have to grow as quickly as possible if they are going to reach the canopy before other trees in the gap and before light and space are reduced by lateral growth of existing canopy trees. Light-demanding species cannot afford to allocate resources to voluminous canopies until they approach the canopy because of the trade-off in the necessity of adding height to stay in the high-light environment, versus adding crown depth to capture more light.

We did not measure leaf area or the location of the leaves in the canopies of individual trees. Therefore, it is not yet possible to conclude that the deeper crowns of shade tolerant species do not form a monolayer because of their leaf arrangement within the crown. It would be worthwhile to determine the architectural model and leaf arrangement of these 50 species and to collect data from more gap dependent species. With these data it would be possible to define more accurately the trade-off in height growth and crown or leaf area growth, and to evaluate more thoroughly Horn's theory in a closed canopy tropical forest.

\*Based on manuscript submitted to *Functional Ecology* by S.T. O'Brien, S. P. Hubbell, R. Condit, S. Loo de Lao, and R. Foster.



# THE SUPPLY-SIDE ECOLOGY OF THE FOREST ON BCI: A ROLE FOR DISPERSAL LIMITATION?

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Seed dispersal sets the stage for population and community dynamics since, where no seed arrives, no recruit will be produced. Despite this fact, few large-scale, long-term projects have monitored seed dispersal in diverse tropical plant communities. In this article, I describe an extensive research program underway on the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), designed to better understand the dispersal phase of recruitment and its relationship to the establishment phase.

On January 1, 1987, Dr. S. Joseph Wright of the Smithsonian Tropical Research Institute (STRI) began monitoring the community-wide rain of plant propagules and reproductive debris in the 50-ha plot on BCI. Just prior to that time, Dr. Wright and field technician José Polanco placed 200 traps along the trail system that snakes through the 50-ha plot (Figure 1). Each trap is constructed from a 0.5 m x 0.5 m PVC frame supporting a shallow, open-topped, 1 mm nylon-mesh bag, suspended 0.8 m above the ground on four PVC stakes.

During the first year of monitoring, Mr. Polanco identified and counted, on a weekly basis, every seed, fruit, and flower > 1 mm that fell into the traps. Osvaldo Calderón took over as the new field technician on January 1, 1988, at which time it was decided to record flowers on a presence/absence basis by species for each trap each week, while continuing to count all seeds and fruits > 1 mm. Together, Mr. Polanco and Mr. Calderón have counted and identified over 1,000,000 items from 450 species of trees, shrubs, lianas, and epi-

phytes!

Dr. Wright's objective in undertaking this project, funded by STRI's Environmental Studies Program, was to better characterize the reproductive phenology of this species-rich plant community. To this end, the project has been quite fruitful.

When I learned of this trapping project, I recognized the potential for using the data to quantify community-wide spatial patterns of the seed-rain within the 50-ha Forest Dynamics Plot, and to understand its consequences for population and community dynamics. Armed with eight years of data, Dr. Wright and I are using the mature fruit and seed data for tree and shrub species to characterize spatial patterns of the seed "input", that is, the supply-side ecology, of the forest on BCI. The most striking results from our analyses have been the small numbers of species found per trap, relative to the tree and shrub community of the 50-ha plot. Over the 8-yr trapping period, we recorded an average of 15 out of 108 (14%) canopy tree species per trap (Figure 2). This observation suggests that dispersal limitation may be an important phenomenon with consequences for the dynamics of this community. That is, viable seeds do not appear to be reaching all sites in which they could produce seedling and sapling recruits.

One might criticize our estimates of the species-richness of the local seed-rain by pointing out that the seed traps miss secondary seed-dispersal by rodents, ants, and others which should homogenize the seed-rain. However, there are also reasons to argue that our method may provide an over-estimate of the species-richness of the local seed-rain. Since seeds were only scored for maturity, but not for viability (despite the prevalence of pests, parasites, and predators that damage seeds prior to primary dispersal), and since many of the species found in a given trap represent a single seed during the

8-yr interval, we may have over-estimated the mean number of species dispersing viable seeds to each trap location.

In 1994, we began a complementary endeavor to the seed-trapping program. The objective of the new monitoring project is to further test the dispersal-limitation hypothesis, as well as the null hypothesis that shade tolerant tropical tree

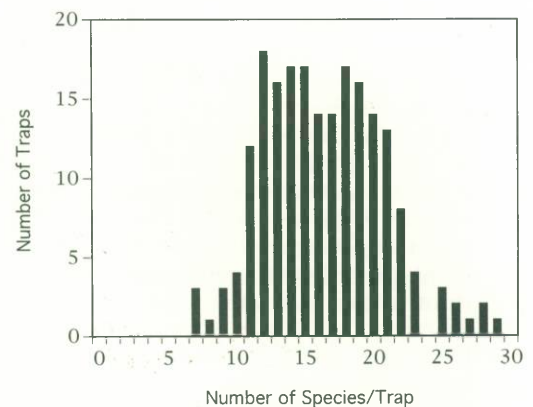


Fig. 2. Histogram of the number of canopy tree species (found as seeds) per trap over the 8-yr period, inclusive (n=200 traps).

seedlings are competitively equivalent. Each year since 1994, during the dry season, Eduardo Sierra has identified, measured, and mapped all seedlings in three 1 m x 1 m plots surrounding, at a distance of 2 m, each of the 200 seed traps. In addition, since the main database for the 50-ha plot only includes stems  $\geq 1$  cm dbh, Mr. Sierra also began censusing saplings (woody stems  $\geq 50$  cm in height and < 1 cm dbh) in 5 m x 5 m plots centered on each of the 200 traps. By comparing the recruit "output" relative to the seed "input" in the community, we will soon be able to address: 1) whether positive correlations exist between seeds/trap and conspecific recruits, thereby providing an indirect test of dispersal limitation, and 2) whether random sampling of the local seed-rain predicts the local composition of recruits, thereby indirectly testing for competitive equivalence at the seedling/small sapling stage. If non-random thinning from the seed to seedling or sapling stage exists, we will be able to conduct appropriate statistical tests to better understand the non-random nature of recruitment.

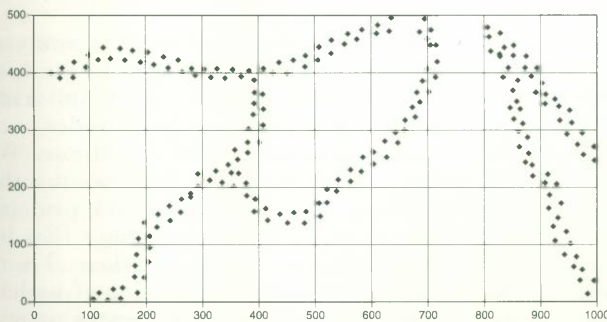


Fig. 1. Locations of the 200 phenological monitoring traps found along the trail system of the 50-ha Forest Dynamics Plot on BCI.